124. [B., P.] Butorides javanica. [E., W.]
125. [B., P.] Gorsachius melanolophus. [W.]
126. [B., P.] Sterna bergii. [W.]
127. Sterna sinensis. [W.]
128. [B., P.] Hydrochelidon hybrida. [W.]
129. Fregata minor. [W.]

XV.—*The Polar Origin of Life considered in its bearing on the Distribution and Migration of Birds.*—Part II. By H. B. Tristram, D.D., F.R.S.

[Continued from 'The Ibis,' 1887, p. 242.]

In suggesting the theory that the Polar origin of life affords a key to the various problems connected with the distribution and migration of birds, I do not think it necessary to go further than I have already done into the question of past changes in the eccentricity of the earth's orbit, since no such change is required to account for the existing conditions of life; and in this, as in every other unsolved problem, the simplest explanation generally proves the best. Nor does it seem to me that we need speculate on the question of various recurring glacial epochs in order to explain the phenomena we encounter. I do not deny the existence of such alternating periods of heat and cold; I merely mean that their introduction as postulates is not required for our present purpose.

I may refer to the summary in my first paper (Ibis, 1887, p. 236), for which I am indebted to Mr. Scribner and Col. Feilden, of the propositions as to the origin of life at the Poles—the first portions of our cooling globe capable of maintaining life. It is, moreover, important to divest our minds of the popular notion that identical or similar forms of life in geologic periods were synchronous. There is abundant evidence, for example, that the Miocene flora of Germany, though in many, or perhaps all, its species identical with the Miocene flora of Spitsbergen, Novaya Zemlya, Grinnel Land, Melville Island, the Parry Islands, Bering's Straits, and Greenland, was in time incalculably posterior to it. By still greater intervals must the strata nearer the equator be separated from similar Polar deposits.

Geologists are agreed that in the Miocene period the North Polar region was a continental area, supporting throughout its extent the same or similar forms of life, as evidenced by the remains found in the districts named above, which may be looked on as the relics of that submerged continent. Here life was generally diffused, and, judging from the fossil plants—the *Magnolias, Sequoias,* and the like—the temperature was that of the present equatorial zone. During the secular refrigeration of the earth the temperature of this continent gradually decreased till it became wholly incapable of supporting such life as we now find in the torrid and temperate zones. There were only two routes of exit for the retreating aquatic and littoral forms: the openings of the North Atlantic and North Pacific Oceans, between Greenland and Scandinavia, and between Kamschatka and the Rocky Mountains. Down these four lines the fauna and flora of every kind steadily, but reluctantly, retired in slow succession, progressing no faster than the modification of the climate demanded. The further they proceeded southwards, the more isolated they became from those which had taken a different route. The law of isolation produced its invariable result, unchecked by that interbreeding which might have arrested departure from the original type. The more sedentary the species, the more marked became the divergence. Those species which were the first to leave—the ancestors of the present tropical inhabitants—became the most differentiated. Those which were the last to leave, and which most persistently revisited their ancestral homes, there associated with their kinsfolk from east and west, and thus preserved the original type throughout the world; as we see in the case of the Knot, the Sanderling, the Turnstone, and many other Waders, which breed generally throughout the Arctic circle. The Gulls, on the contrary, never going far from the open sea to breed, commingled very little, if at all, with their congeners from the other oceans, and their conditions of life being identical, whether in the Atlantic or Pacific, the changes were but slight in corresponding species of either ocean, notwithstanding their segregation in their breeding haunts.

Meanwhile, as the Polar continent continued to cool, the accumulation of snow and ice over its whole surface became so enormous from the precipitation of frozen vapour, as to equal the present deposits on the Southern Polar continent. The continuous land area prevented the circulation of the equatorial currents round the Pole. This was going on throughout the Pliocene era. The glaciers pushed down across the Atlantic in the latitude of the British Isles, and formed a complete barrier from America to Europe. At length the superincumbent mass on the Polar continent pressed down that area below the sea-level, with the exception of the higher lands, which became islands. The glaciers sank to the edge of the ocean. The equatorial current did its work; the ice-blocks became detached, the ancient land behind them was now submerged. The warm Atlantic stream burst in towards the Pole, and the glacial epoch gradually melted away. But with this influx of warmer water, the submerged land, relieved of its superincumbent weight, gradually began to rise again wherever touched by the equatorial current. This process we see going on before our eyes in the elevation of Scandinavia, and the still more rapid upheaval of Spitsbergen, Grinnel Land, the Parry Archipelago, and Novaya Zemlya which has risen 100 feet in less than 300 years. Meanwhile Greenland, struck by the Polar instead of the equatorial current, and overpowered by the weight of its glaciers and ice-deposits, is as steadily sinking. But this process of the glacial epoch, with the phenomena and results of which we are so familiar, appears to have been confined to the region between Hudson's Bay and the White Sea. There does not seem to be any clear evidence that there was any synchronous period of gelation, either in Northern Asia or in America west of Hudson's Bay. Geikie limits the extension of the ice-age in Europe to the north and central portions as far as Saxony, the Alps, and Pyrenees; and in America to Canada and the eastern States as far as the 39th parallel of north latitude. Nordenskiöld, in the "Voyage of the 'Vega'," repeatedly remarks upon the evidence which Siberia affords that it has not been subject to any great geographical changes since the Jurassic period (vol. ii. p. 209, &c.), and he writes of the shores of the Arctic Ocean:—"It is certain that the ice-cap did not extend over the plains of Siberia, where it can be proved that no ice-age, in a Scandinavian sense, ever existed, and where the state of the land from the Jurassic period onwards was indeed subjected to some changes, but to none of the thoroughgoing mundane revolutions which in former times geologists loved to depict in so bright colours. At least the direction of the rivers appear to have been unchanged since then. Perhaps even the difference between the Siberia where Chikanovski's *Ginko* woods grew and the mammoth roamed about, and that where now, at a limited depth under the surface, constantly frozen ground is to be met with, depends merely on the isothermal lines having sunk slightly towards the equator" (vol. ii. p. 246). All the evidence tending to show the limited area of the glacial epoch proves,—first, that we have no need to invoke changes connected with the eccentricity of the earth's orbit, for then the extension of the ice-clad region would have been circumpolar, instead of being grouped round the North Atlantic; secondly, that we need not invoke the glacial epoch at all, still less an indefinite number of glacial epochs, to account for the present phenomena of distribution and migration, for then the solution would apply only to the Atlantic distribution; while, dismissing these disorderly interruptions, the secular refrigeration of the globe suffices for all.

Confining myself, as in the pages of 'The Ibis' I am bound to do, to the avifauna exclusively, and abstaining from the attractive illustrations of the subject afforded by the Mollusca, and still more by the Flora, I would venture to sugest that the gradual refrigeration is sufficient of itself to explain the distribution of species, and to account for the phenomena of migration. We have assumed that there were but three principal lines of migration southward. Why, it may be asked, should we assume these special lines? Why may not the exiles have departed over land in any direction? That the fourth coast-line, down the east of North America, was unimportant—if followed at all—appears from the fact that the central area of North America was at that period the basin of a vast shallow sea, with, perhaps, a few islets; and that south of New England the land continuity must have been broken. And as to the departing overland in any direction, our hypothesis assumes the heredity of habits, and we know that for the most part migrants, where possible, hug the coast-line or follow the bases of mountain-ranges. Assuming, too, the reluctance of the first exiles to move, this being also founded on the heredity we now observe, they would be shut out by the frost from the interior lands, and would congregate on the river-banks and along the shores for food, as many of our native non-migrants do now—*e. g.*, the Rook—before they finally took flight for the south. On all these questions connected with distribution and migration the various papers of Mr. Seebohm in 'The Ibis' and elsewhere have been most instructive, and he has dealt with the subject at much greater length in his new work on the Waders, of which he has kindly allowed me to see the advanced sheets. I am aware that Mr. Seebohm invokes glacial epochs and alternations of climate extending over enormous eras uniformly in the circumpolar area to explain the present distribution of bird-life, and that he would also attribute to some—as to the *Hirundinidæ*—a South Polar origin. I am not prepared to contest his theory of past geologic history, but only to submit that they are not necessary for our solution.

I have in my former paper taken the distribution of the *Picidæ* and of *Pica* as illustrations. Before adducing other groups, I may, perhaps, be allowed to lay down certain generalized deductions on migration and distribution:—

1. That all birds breed at the northernmost limit of their range.
2. That those which penetrate furthest north for nidification, whether species or individuals, usually retire furthest south.
3. That all northward migration is for the purpose of nidification; the southward being for food or warmth.
4. That the lines of migration are very different in the case of different species, and often intersect each other.
5. That birds which breed in the tropics do not migrate, unless in the case of birds which ascend the mountains for nidification, and descend to the plains in winter, as various Thrushes in the Andes, and numberless species in the Himalayas.

If it be asked, why, on the doctrine of heredity, should not all birds migrate for nidification? I would reply that these tropical *genera* are the descendants of those which left the Poles at a much earlier period than others, before their structure or habits had become in any degree adapted to the decreasing temperature, and therefore steadily retreated as the cold increased. Take, for example, the great family of the Humming-birds, one of the most differentiated in our avifauna. The ancestors must have left the Pole by the western shore-line of N. America. They may have been confined originally to the portion of the old Arctic continent nearest Bering's Straits, or the parties which took the other routes have perished and left no trace behind. Working southwards they threw out colonies, especially to the eastward, and peopled the Antilles, where, as further south, the sedentary parties soon became differentiated. Still following the retreating warmth, they settled in tropical South America, and being a forest- and mountain-loving race, they clung especially to either side of the Andes. The vast eastern plain-region of the Amazons was then probably too hot for them. Some remained at different altitudes of the mountain-ranges, segregated in little groups, venturing neither to face the heat of the plains nor the increasing cold of their northern cradle. But the southern plains were then much hotter than at present. Some therefore daringly pushed towards the extremity of the continent. Those which struggled as far as Juan Fernandez remained isolated, having reached it after the instinct of migration had been weakened by desuetude, and so became distinct and sedentary species, accommodating themselves to the reduction of temperature. Those which kept to the line of the continent and reached Tierra del Fuego, like *Eustephanus galeritus,* retreated again as the temperature fell in winter, and became one of the few exceptions to the rule of northward migration for nidification. A similar modification was induced in the sedentary species of the Andes as the climate cooled; till now some may be found near the snow-line, while others are almost confined to a single crater. But while species multiplied by segregation, whether in islands or on mountain-sides, there were those which never lost their hereditary attachment to the north; and so we find on the one side *Trochilus colubris* pushing its adventurous journey as far as Labrador, and on the other *Selasphorus rufus* up to Nootka Sound. We can scarcely account for the prodigious annual expeditions by these tiniest specimens of bird-kind on any other principle than that of heredity. It cannot be climate nor the search for suitable food which impels them; for both suitable food and temperature are to be found thousands of miles nearer their winter-quarters. I think, too, that the case of these two Humming-birds disposes of the hypothesis of an acquired habit. No such habit could be acquired unless it were for the benefit of the species, and the loss of life from storm and enemies during this expedition of over 3000 miles must be prodigious. The fact of these two species taking such divergent routes on either side of the continent seems to indicate a very early dispersal of the family over the neotropical area.

The Thrush tribe is, perhaps, the most universally distributed of the Passerine family. Taking what we may call the true Thrushes—*i.e.* Mr. Seebohm's genera of *Geocichla, Turdus, Merula, Mimocichla, Catharus,* and *Monticola*—we find the group represented in every region and in every district of every region of the world, excepting in New Zealand. In habits the species vary from the widest limits of migration to the most limited localization. It would seem as though the progenitors had pursued every available route as they retired from the Pole. But the most southern and sedentary species have indisputably a northern origin. Take, for instance, the Blackbird. We find, to mention only a few species out of many, in Western Europe, in Eastern Asia, in the mountains of Ecuador, in the Samoa Islands, *Turdus merula*, *T. mandarinus*, *T. serranus*, and *T. samoensis*, all Blackbirds, differing only in size and in some slight peculiarities, such as the colour of the legs. These must have had a common ancestry, whose progenitors, we may suppose, had become differentiated from any other type of *Turdidæ* before they left the Polar continent. It is impossible to conceive that *T. serranus* and *T. merula* were derived the one from the other, or that the two have ever been in contact since their progenitors left their ancestral home. But if there were a Blackbird generally spread over the Arctic continent, and dispersed, partly down the East Atlantic line, and partly down the east and west coasts of the Pacific, the progenitors of *T. serranus* and its neotropical congeners must have travelled down by the Rocky-Mountain range, till, reaching the higher Andes, they found on the mountain-slopes the changes they required, and substituted a vertical for a latitudinal migration, according to the season. Similarly, the progenitors of *T. merula* spread over Europe and became migratory to a very limited extent; while a third party, skirting Eastern Asia, followed the mountain-ranges from China westward; and became slightly differentiated, as they settled in various districts, into the numerous species of Blackbirds of Eastern Asia. Some of this party, more adventurous than their fellows, appear to have crossed into Formosa, and there slightly dwindling in size, partially acquired that white plumage so often characteristic of insular forms, and became the White-headed Blackbird, *T. albiceps*, of Formosa. From this adventurous race seem to have sprung the many species inhabiting the Pacific Islands, of which some thirteen have been already described, varying from black to brown, some with grey, ashen, or buff heads; but all small of stature, and all having an unmistakable family resemblance, and all sedentary in their respective islands. But the Blackbirds were among the last of the *Turdidæ* to leave the far north. They had become comparatively acclimatized, as well as differentiated; and in this way we may account for the absence of this group of *Turdidæ* from the Ethiopian fauna, the Blackbird finding the temperate climate of Europe adapted to its needs, and being therefore not tempted to push further south than the Mediterranean coasts. At the time of the emigration of the Blackbirds the accumulation of ice may have commenced in the glacial epoch on the West Atlantic coast, and consequently no species of this group occur in North America.

But there were probably two previous principal epochs of emigration of the Turdidæ from the north. The first and earliest would seem to have been that of the genus *Oreocincla*, the least differentiated of the family. These earliest emigrants only made a partial exodus, and that down the line of Eastern Asia. They seem to have emigrated before the family had become sufficiently differentiated to lose in maturity the spotted plumage of the young. As is well known, all the *Oreocinclæ*, alone of this family, retain the same markings through life. Some of the emigrants soon halted, penetrating no further than Japan and China. These retained their attachment to the place of their origin; and to this day *Oreocincla varia*, while retiring even as far as the Philippines in winter, returns to Siberia for nidification. From China one party penetrated to the Himalayas and sent colonies along the central mountain-ranges down to Ceylon. All these soon learned to content themselves with a seasonal vertical migration, like the subsequent settlements of Blackbirds. Others reached Formosa and there remained, while others, finding the plains and valleys too hot, pushed further south, even to Australia and Tasmania, leaving a few settlers on each island on their route, which have gradually become specifically or subspecifically distinct from long isolation: Java, New Guinea, Timor Laut, N. Australia, S. Australia, Tasmania, and probably other islands, possessing their recognized sedentary varieties, but all mountaineers in the breeding-season.

Next, but long after, when the family within the Arctic continent had learned in some degree to adapt itself to the diminishing temperature, and had, at the same time, modified its adult plumage, the great mass of the Thrushes were driven southward on the second or great migration. The retreating parties would seem to have followed all the possible lines of retreat, and many of them to have boldly crossed the ocean north of Siberia and followed up the course of its mighty rivers. Many remained in the north, some of whom, represented by our Fieldfares and Redwings, clung most pertinaciously to their homes, and went no further than compelled by dire necessity. Others, among them the ancestors of our Song Thrush and Missel Thrush, adopted various routes, but principally the East Atlantic and the Siberian rivers, and returning north each year, have, by mutual intercourse, maintained across Europe and the greater part of Asia the ancestral type unchanged. Again, a considerable portion of these migrants, following down the west of Africa, spread eastward over that continent, and, their return being barred by the Saharan desert, became strictly sedentary in their various localities, where they have become differentiated into some dozen species. A straggler or two of this adventurous flight reached even Tristan d'Acunha, where his wings were so clipped that he abandoned all thought of foreign travel; until now some of his friends refuse to recognize him, and would have us believe that he is no Thrush, but a Timaline.

The small size, the spotted breast, the strong generic affinities of the Nearctic Thrushes, and their marked distinction from all the South-American species, would lead me to believe that they are descendants of ancestors which peopled N. America by way of Greenland and Labrador: probably at a period when the central area was submerged. They have all retained their hereditary attachment to the north, and the extent of their migration from their winter in the tropics to the shores of the Arctic Ocean is not surpassed by any land-bird.

A far more important body of colonists was that which worked down Western America to Panama and then divided eastward and southward. From these spring the bulk of the neotropical Thrushes, which, with the exception of *T. migratorius*, seem to have lost, from isolation, the habit of any save vertical migration; while others, as *T. falklandicus*, are, from circumstances, strictly sedentary. But those which followed the eastward route from Panama afford a remarkable instance of the effects of isolation. We have first the continental group of Mexico and Central America, forming the recognized genus *Catharus*; all the species of which are, so far as we know, sedentary. For this exception I can suggest no explanation, unless that their ancestors, baffled by the submerged area of the now Mississippi valley, abandoned the effort to revisit the north. In the case of the colonists of South America, we must remember that, travelling south by the lofty Andean ranges, they would escape the then intolerable heat of the lower equatorial regions, and that when once settled on the side of the mountains or in the temperate southern regions, the heat of the equatorial belt might repel their efforts to revisit the north. Perhaps the most interesting development of all in this family is that of the *Mimocichlæ* in the Antilles. These certainly have a common origin, and seem to come most naturally as among the results of this great migration. Each species is confined to a single island, and they certainly must have been differentiated where they now are. I am not at all certain that we ought not also to include among these results the *Cichlherminia* group of the Lesser Antilles. It is certainly remarkable that, whether in the Pacific or West Indies, a species which has once bred in an island, even the smallest, seems always to lose its migratory instinct, however strongly that habit may be impressed on the family generally.

A large party of emigrants must have chosen the East

Pacific route, by Kamschatka and Japan. All the East-Asiatic species, some thirteen in number, with the doubtful exception of *T. javanicus*, appear to be strongly migratory in their habits; all reverting to N.E. Asia for nidification, and thus indicating the route by which their ancestors first set forth. It is very possible that these species, as well as many of those which adopted other routes, had become segregated before their final departure from the Arctic continent. Mr. Seebohm would explain this by the theory of successive emigrations during successive glacial epochs, the species being developed in different southerly regions during isolation from kinsfolk, and then returning with the retrocession of the ice. The species now having become perfectly distinct, set forth again at the next glacial epoch, each of those species being the generic progenitor from which many existing species have evolved. Without denying the possibility of this hypothesis, I think that one partial glacial epoch may explain approximately the existing conditions of the Thrush family.

I have taken the Thrushes as one illustration, and I think a similar method might be applied in the treatment of all the principal families. I do not think that there is any evidence of a South-Polar origin for any of our land-birds, any more than for any of our Flora above the lowest cryptogams. I have already, in my last paper, admitted the probability of the southern origin of the Penguins—a conjecture strengthened by the recent demonstration of the structural difference between the wing-feathers of this and any other known family. Perhaps the Petrels might be added as of probable southern origin; by far the larger proportion of species being inhabitants of the Southern Ocean, while the curious habit of nesting in burrows near the tops of mountains, away from their ordinary haunts, may have been derived from the absence of any low-lying land in the Antarctic continent.

A southern origin has also been suggested for the Swallows. I fail to see the force of the arguments in support of the hypothesis. All Swallows, like all other birds, breed at the northern limit of their range,—a fact, the origin of which I propose to explain by the heredity of attachment to their place of origin. It is true that there are many more species of Swallows which breed in the southern than in the northern regions. But these are simply, like the Ethiopian and Neotropical Thrushes, races which have become sedentary, and thus been specialized into local species. In the countries in which these local species are found, the individuals of the migratory sorts, spending our winter in South Africa, exceed ten-fold or fifty-fold the number of all the sedentary species. Why should this be, but because the continued habit of reversion to the north, and the intercourse with their fellows from other southern regions whom they there meet, have secured permanence of type and checked the tendency to variation by segregation which marks the permanent dwellers in Southern Africa? If the Hirundinidæ had had a southern origin, how could the habit of northward migration have originated? Not certainly by imitation, for their flight is more rapid than that of most other travellers. Not from absence of food in the south, for where the sedentary species can find support so could the migratory. Besides, as we know, in the case of *Hirundo savignii* and *Cotile rupestris*, there are sedentary species in the north as well as in the south.

If the Swallow tribe had a southern origin, there has been no theory yet advanced on migration which could possibly be reconciled with the facts of its life-history. Genera are but arbitrary divisions, and the fact that of the eleven genera of Hirundinidæ, most of which are very unsubstantial and shadowy abstractions, only one is cosmopolitan, and that now *confined* to the Palæarctic Region, rather goes to illustrate the enormous powers of flight of the family, and the ease with which so great a change as that from a roving to a sedentary life has modified the specific characters of the group. The one fact that none of the migratory Hirundinidæ breed in the southern hemisphere, though visiting it at the times of the nidification of the local species, seems to be of itself proof enough of a northern origin.